Review

Biome diversity in South Asia - How can we improve vegetation models to understand global change impact at regional level?

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HIGHLIGHTS

- South Asia's rich biodiversity is threatened by climate change and land use.
- Understanding climate-human-biodiversity interactions requires predictive models.
- We propose a research agenda to better represent South Asia's vegetation in models.
- Models need to represent trait variability, diversity and evolutionary principles.
- Improvements will facilitate development of adaptation and mitigation strategies.

GRAPHICAL ABSTRACT
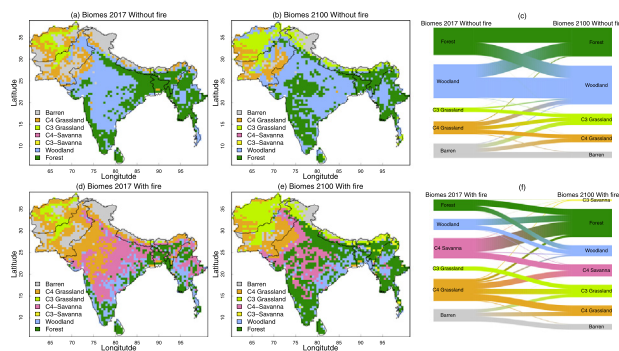
ABSTRACT

The distribution of biomes in South Asia is expected to be affected severely by climate change. Understanding plant-climate interactions and the impact of climate change, rising CO_2, land use change, deforestation and fire on vegetation has become a major challenge for ecologists. Therefore, developing the capacity to project vegetation change is of critical importance if we are to mitigate and efficiently adapt to climate change impacts. The lack of an accurate representation of different vegetation types and ecosystem processes at regional scale is a main source of uncertainty in Dynamic Global Vegetation Models (DGVMs). This manifests in a lack of key growth forms such as bamboo, lianas and mangroves and biome types such as savanna which are essential components of ecosystems in South Asia. Plant communities like mangroves and bamboos, despite covering just small areas, account for high carbon sequestration whereas lianas can decrease carbon sequestration capacity of host trees. Here, we review the current state of vegetation modeling for South Asia and we propose a research agenda for an improved representation of biome diversity in DGVMs. We account for both the traditional plant functional type (PFT) approach and for the functional trait (FT) approach that considers growing knowledge on plant-trait variability and eco-evolutionary principles of different plant communities. We argue that an adequate representation of different vegetation types and growth forms characteristic of South Asian biomes is necessary in DGVMs for robust assessments of climate change impacts on their distribution, diversity and carbon budget.

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Contents

1. Introduction

Interactions between climate and vegetation at the local scale influence the ecology, structure and distribution of biomes (Quillet et al., 2010). For decades ecologists have recognized climate as a primary determinant of large-scale vegetation distributions (Greve et al., 2011; Walter, 1985). Yet, the relationship between climate and vegetation patterns is not necessarily deterministic (Murphy and Bowman, 2012; Zeng et al., 2013) and similar climate conditions can support different plant communities. Knowledge of climate-vegetation interactions is particularly important in highly heterogeneous environments such as the tropics of South Asia (Cho et al., 2015; Gautam et al., 2013; Wang et al., 2017). South Asia comprises steep gradients in climate, topography and soil, all of which influencing heterogeneity of biome patterns (Tripathi et al., 2017). Evolutionary history and multi-stability of different biome types further contribute to this complexity (Cadotte et al., 2008). Understanding the complexity of South Asian geography and plant species richness (Chitale et al., 2014; Panda et al., 2017) is a unique challenge to biogeographers and ecologists (Katayama et al., 2014; Squires, 2014). However, general explanations for the rich diversity and tools to project past, current and future biome patterns at high spatial resolutions are still not sufficient.

Biome diversity in South Asia is threatened by both climate change (Chitale et al., 2014; Hooper et al., 2012; Parmesan and Yohe, 2003) and land use impacts (Foley et al., 2005; Newbold et al., 2015; Pandit et al., 2007). Recent decades showed dramatic losses of species in many South Asian ecosystems and degradation of biodiversity. For instance, Pandit et al. (2007) documented that deforestation has reduced the number of endemic species in the Himalayan ecosystems. It has been predicted that Asia could lose three quarters of its original forests, and half of its biodiversity by 2100 (Deb et al., 2017; Deb, 2017; Sodhi et al., 2004). This might cause a decrease in resilience, and eventually drive the extinction of rare and endangered tree species in the region (Allen et al., 2014; Deb et al., 2018).

Ecosystems supply a range of ecosystem goods and services to people, such as food, wood for heating, cooking and construction, carbon sequestration, ecotourism or biodiversity (Parr et al., 2012). The increasing pressure of the human population in South Asia has serious consequences for the provision of ecosystem services. In some regions, deforestation has resulted in a rapid invasion of alien plants such as

Lantana species (Sharma et al., 2005b). These species can negatively affect nutrient cycling (Ramaswami and Sukumar, 2016) and prevent regeneration of native forest species by decreasing germination success and growth rates in a plant's seedling (Sharma et al., 2005a, 2005b). Invasive *Lantana* species may lead to a decline of native trees and a reduction of forest diversity and carbon sequestration. To counter deforestation, the Indian government has established a large afforestation program (Ravindranath et al., 2008). Yet, government policies for afforestation of non-forest lands pose a threat to biomes such as savanna (Ratnam et al., 2016) and grassland.

Predicting the potential effects of future climate change and human impacts on vegetation dynamics require large-scale bio-geographical models (MacDonald et al., 2008; Root et al., 2005). There are two basic approaches to modeling vegetation response to climate change: static (time-independent) and dynamic (time-dependent) vegetation models. Static models predict the distribution of potential vegetation by relating the geographic distribution of climate parameters and vegetation, with the assumption of equilibrium conditions for both climate and vegetation. Such climate envelope models or species distribution models are typically based on statistical methods (Franklin, 2010). Dynamic processes are generally ignored (Peng, 2000). Static models do not consider the impact of changing atmospheric CO_2 concentrations (Kearney and Porter, 2009; Linder et al., 2012) and also ignore succession and evolution (Hughes et al., 2013; Mucina and Rutherford, 2006). On the other hand dynamic models such as DGVMs are based on mechanistic process and include time-dependent processes such as growth, establishment, competition, mortality and disturbance (Cramer et al., 2001; Prentice et al., 2007). Yet, most DGVMs do typically not represent the diverse vegetation of South Asia, for instance savanna, mangroves, bamboos and dry deciduous forest. Recently, Ratnam et al. (2016) demonstrated that most of the southern part of the Indian subcontinent is savanna. We claim that we need a better understanding of vegetation patterns in South Asia as well as of the underlying processes and environmental drivers, so that we can predict vegetation distributions under projected climate change and deduce adaptation mechanisms to mitigate the consequences of global change (Jones et al., 2009; Negi et al., 2012). Here, we review the state-of-the-art in process-based vegetation modeling for South Asia and we identify knowledge gaps, in particular with respect to vegetation types and growth forms not accounted for in DGVMs. We then provide

suggestions how to implement these missing vegetation types and growth forms to reduce uncertainty of DGVMs in the study region.

2. South Asia's biome diversity

South Asia covers 5 million km^2 and is bounded by the Indian Ocean in the south and the Himalayan mountain range in the north. The meteorological conditions are controlled primarily by the movement of the inter-tropical convergence zone (ITCZ, Patra et al., 2013). South Asia experiences dry seasons without rainfall during autumn, winter and spring when the ITCZ is located over the Indian Ocean (between the Equator and 5° S), whereas the region receives about 70% of total annual precipitation during summer (June to September) when the ITCZ is located north of the equator (Patra et al., 2013). Climatic conditions vary from arid in the west to humid in the east and temperate in the north to tropical in the south. Elevation ranges from sea level in peninsular south India to 8500 m in the Himalayas. Elevation gradients are associated with steep temperature gradients and a variety of soil types and topographies. South Asia's topography consists of different mountain ranges, plateaus, dry regions, river basins and humid regions.

The complexity of environmental conditions has resulted in a rich diversity in biome types (Ramankutty et al., 2010, Fig. 1(a)), with deserts to grasslands in the northwest, savannas on the Indian peninsula, tropical deciduous and evergreen forest in the Western Ghats and eastern India as well as lowland and montane forests in the lower Himalayas. The region hosts five of the fourteen major ecological regions or biomes of the world. These biomes harbor different ecosystems which are the result of unique combinations of abiotic factors such as climate, geology, soil and diverse topography. Some of the biomes in India and Myanmar host remarkable biodiversity and are among the major biodiversity hotspots of the world (Myers et al., 2000).

South Asia is one of the world's most densely populated regions, accordingly, a large fraction of the area is utilized for cultivation accounting for nearly 1 million km^2. Non-forested areas like grassland, savanna, barren and shrubland account for 0.35 million km^2, 0.22 million km^2, 1.5 million km^2 and 0.89 million km^2, respectively (Defries and Townshend, 1994; Patra et al., 2013). Forested areas are classified as broadleaf evergreen, broadleaf deciduous and mixed coniferous and account for 0.11 million km^2, 0.10 million km^2 and 0.05 million km^2, respectively (Defries and Townshend, 1994; Patra et al., 2013). About 18.6% of the total land area of the region is still covered by forest and it accounts for 1.98% of the total forest area in the world (http://www.fao.org/docrep/004/y1997e/y1997e0s.htm#fn39). In India, 21% of the area is classified as forest (FSI, 2017) with tropical forests accounting for approximately 86% of the forested area (Singh and Singh, 1988).

3. South Asia's contribution to the global carbon cycle

South Asia has undergone rapid economic growth over the past two decades, which has been associated with significant changes in the rates of land-use change and large increases in fossil fuel emissions (Cervarich et al., 2016; Patra et al., 2013). Land-use changes reshape landscapes and may cause substantial environmental risks. For example, land-use change causes accelerated carbon and greenhouse gas emissions (Foley et al., 2005; Houghton, 1999; Kaye et al., 2004; Tian et al., 2010), change in surface fluxes (Feddema et al., 2005; Pielke, 2005; Snyder, 2010; Zhang et al., 1996) and land degradation (Drake and Vafeidis, 2004; Thornes, 1996). Some of these consequences ultimately lead the loss of biodiversity (Pimm et al., 1996; Sala et al., 2000).

The tropical terrestrial ecosystems of Asia, including South and Southeast Asia, play a crucial role in regional and global carbon cycling (Brown et al., 1991; Flint and Richards, 1994; Houghton, 2002; Tian et al., 2003). In the majority of the region where deforestation occurred, forest land was primarily converted to cropland which will significantly reduce carbon storage in the terrestrial ecosystem (Achard et al., 2004, 2002; Canadell, 2002).

A study using an inversion ensemble method, found that the land biosphere in South Asia was close to carbon neutral, with an annual flux of −0.05 (−0.18 to 0.03) PgC per year for 1996 to 2012 (Thompson et al., 2016). The terrestrial net biome productivity calculated based on bottom-up models in combination with emissions from fire based on the Global Fire Emissions Database version 4.1 (GFED4, Van der Werf et al., 2010) show net carbon sink of 217 ± 147 TgC yr^{-1} for South Asia (Cervarich et al., 2016).

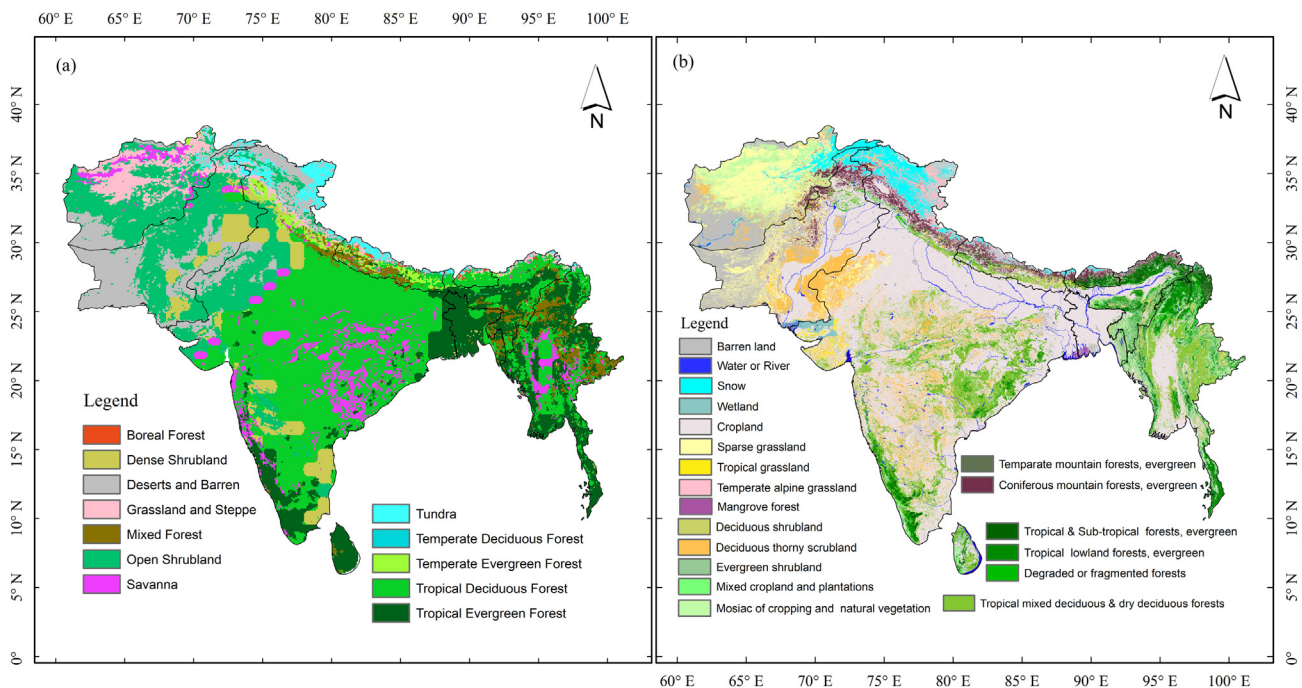**Fig. 1.** (a) Major potential natural vegetation types of South Asia (ISLSCP-II, Ramankutty et al., 2010) and (b) Global land cover map (GLC2000, http://forobs.jrc.ec.europa.eu/products/glc2000/glc2000.php). The ISLSCP-II data product was derived from the land cover data set of Loveland et al. (2000) following the Olson Global Ecosystems (OGE) framework (Olson, 1994) classification scheme.

To compensate for greenhouse gas emissions, afforestation initiatives have increased the forest extent in South Asia by ca. 3% (2.1 Mha) between 1990 and 2010 (FA0, 2010; Thompson et al., 2016). India alone has increased the extent of forest through plantations by ca. 7% from 1990 to 2010, leading to a 26% increase in carbon sequestration in living forest biomass (FA0, 2010).

Quantifying the region's terrestrial carbon budget and related carbon fluxes would help to determine carbon sequestration capacity of its forests and other ecosystems.

4. Anthropogenic impacts in South Asia

South Asia is home to well over one fifth of the world's population, making it the most densely populated region in the world. Increasing demands for resources due to a population explosion are the driving force behind deforestation (Singh et al., 1991) and land transformation, mainly into cropland, resulting in biodiversity loss (Vitousek et al., 1997; Cincotta et al., 2000). In India, the largest country in South Asia, nearly 173,000 villages are classified as forest villages. Communities in these forest villages largely depend on the natural resources that ecosystems provide (Kishwan et al., 2009) and human activities alter forest biomass and plant community composition (Agarwala et al., 2016). In the eastern part of South Asia, population density has been increasing steadily over the past decade at a rate of 1.5% per annum (United Nations Statistics Division, 2007), implying that remaining forests will continue to face high risk of degradation both locally, and over the entire region.

Another common anthropogenic activity in the region is the practice of slash and burn, also known as shifting cultivation; it accounts for 49% of forest degradation in tropical Asia (Ruangpanit, 1995). Cutting and burning forests alters the natural fire regime and inhibits time to recover, which further degrades ecosystems and causes more carbon emissions in the region. This practice leads to land transformation, allowing spread of invasive species which often grow faster than local species and out-compete the local flora (Rai and Singh, 2015). Nevertheless, the slash and burn practice is intricately linked to the culture and livelihood of communities in the Eastern part of South Asia (Ramakrishnan, 1992). The sustainability of this practice has been questioned by many ecologists (Karthik et al., 2009) while others support the practice (Raman et al., 1998).

Changes in land use policy aim to mitigate land degradation. For instance, under programs such as Green India mission and Compensatory Afforestation Fund Management and Planning Authority (CAMPA) more area is likely to be afforested. Afforestation improves provision of certain ecosystem services (e. g. carbon sequestration), but these secondary forests are typically different from primary forest in terms of growth rates and biodiversity and they support fewer species than primary forest (Bremer and Farley, 2010; Wang and Cao, 2011).

Another significant anthropogenic factor which has become a major issue is the ozone pollution or ozone depletion. Exposure of vegetation to ozone reduces photosynthetic rates (Reich and Amundson, 1985) and plant growth, and alters the plant's mechanism of ozone response (Mauzerall et al., 2001) such as stomata regulation (Felzer et al., 2007; Karnosky et al., 2005, 2003). Plant leaves suffer visible injury due to exposure to ozone (Krupa and Manning, 1988; Somers et al., 1998). Exposure to ozone affects the amounts of carbon sequestered in vegetation and soils, and the harvestable portions of crops (Reich, 1987; Reich and Amundson, 1985). The complex interactions between ozone and stomata regulation (Felzer et al., 2009; Jensen and Roberts, 1986) impair the stomatal function and reduce formation of roots in young and mature vegetation (McLaughlin et al., 2007). This competitive interaction in natural environments often leads to a dominance of ozone-tolerant species, reducing the diversity of the community. The development of flux-based models linked to effects on carbon assimilation and allocation offer a basis to improve the capacity for risk assessment (Felzer et al., 2007), but there is a range of potential impacts of ozone, especially

at the ecosystem level, for which the necessary mechanistic understanding does not exist to allow the inclusion in local or global risk assessments (Ashmore, 2005). Ozone is a key challenge toward understanding the carbon sequestration effects on natural ecosystems.

5. Dynamic global vegetation models (DGVMs)

DGVMs simulate ecological processes to assess climate-vegetation interactions and distributions of vegetation types in response to biotic and abiotic conditions. They are often linked with carbon and nitrogen cycles to simulate biogeochemistry and plant physiological processes, including growth and decay (Bachelet et al., 2001). DGVMs include environmental factors such as climate, soil properties, atmospheric CO_2 concentration, or disturbance regimes (fire or herbivory, Bond and Midgley, 2012; Hoffmann et al., 2012). Traditionally, DGVMs simulate functioning and distribution of predefined plant functional types (PFTs), i.e. groupings of species with similar physiological and ecological functions (Prentice et al., 2007; Woodward et al., 2001). PFTs use a finite set of static parameters to aggregate traits of individual plants with similar functions in an ecosystem, and similar responses to environmental conditions such as water and nutrient availability (Díaz and Cabido, 1997; Kattge et al., 2011; Lavorel et al., 1997). Some DGVMs simulate individual species instead of PFTs (e.g. Hickler et al., 2012).

The PFT schemes used in contemporary DGVMs have been successful in representing global biogeographic patterns. Yet, they usually do not represent vegetation heterogeneity in plant communities at regional scale and ignore much of our growing knowledge of comparative plant ecology (Harrison et al., 2010). The PFT approach often implies a simplistic representation of competition (Fisher et al., 2010; Quillet et al., 2010), because competition is modelled between PFTs and not between individual plants (Clark et al., 2011). This issue has recently been addressed by using Functional Trait (FT) approaches in DGVMs to simulate trait variation in plant communities (Pavlick et al., 2013; Sakschewski et al., 2015; Scheiter et al., 2013; Verheijen et al., 2015; Yang et al., 2015, 2016). Yet, this increased level of detail in models requires large amounts of data on plant-trait variability and eco-evolutionary principles of plant communities for parameterization. Increased model complexity further implies increases in model computation times. We argue that there is need to revisit PFT schemes in DGVMs and to identify key traits and processes required in FT approaches and ultimately to better account for different plant communities in South Asia. The generalization of plant representation and ecosystem processes by DGVMs results in uncertainty of vegetation dynamics at regional scale and in our projections of future vegetation. Harper et al. (2016) showed that using a trait-based representation of PFTs could increase confidence in the simulations of vegetation and carbon dynamics.

6. Current status of vegetation modeling in South Asia

Most global scale DGVMs have a generic representation of various vegetation types, for example tropical areas are typically represented by few PFTs (Snell et al., 2013). They are optimized to reproduce overall patterns, temporal variability and carbon stocks of vegetation and soil at global scale, but do often not provide reliable estimates at regional scales (Tang et al., 2010). Many tropical vegetation types characteristic of South Asia, such as mangroves, xerophytes, montane vegetation, and growth forms such lianas, bamboos and shrubs are not or not adequately included in most DGVMs (but see for example Gaillard et al., 2018 for shrubs or Verbeeck and Kearsley, 2016 for lianas). These vegetation types and growth forms may be critically altered by future global change (Kumar, 2000; Berger et al., 2008).

South Asia exhibits substantial heterogeneity in vegetation cover and needs explicit representation in DGVMs. Most previous DGVM studies for the South Asia focused on impacts of different climate change scenarios on Indian forests (Chaturvedi et al., 2011; Gopalakrishnan

et al., 2011; Ravindranath et al., 2006). These studies revealed shifts in forest boundaries (Chaturvedi et al., 2011; Gopalakrishnan et al., 2011; Ravindranath et al., 2006) and changes in forest productivity (Ravindranath et al., 2011) by the end of century. The upper Himalayas, central and northern parts of the Western Ghats, and parts of central India are projected to be the most vulnerable to climate change, whereas forests in the north-eastern region of the country are more resilient (Chaturvedi et al., 2011; Gopalakrishnan et al., 2011). Two regional studies focusing on potential impacts of climate change on forests in the north of Himachal Pradesh (Deshingkar et al., 1997) and in the Western Ghats (Ravindranath et al., 1997) indicated moderate to large-scale shifts in forest types with implications for forest dieback and biodiversity.

Vegetation models serve as tool to simulate vegetation-climate interaction and their output could be used for better management of ecosystems in future. We ran simulations with aDGVM (Scheiter et al., 2012; Scheiter and Higgins, 2009), a dynamic vegetation model originally developed for African savannas, for South Asia. We found that the IPCC RCP 4.5 climate change scenario affects simulated future vegetation patterns, especially along the Himalayas and Western Ghats by the end the century (Fig. 2). In these simulations, the presence or absence of fire shapes the extent of forest and savanna in South Asia (Fig. 2a, d). While aDGVM broadly simulates patterns of forest, savanna, grasslands and woodland it does not represent dry and moist deciduous forest type and mangroves as well as growth forms such as shrubs and bamboos.

7. Current challenges in vegetation modeling

Models applied at regional scale for South Asia range from statistical species distribution models (Pearson and Dawson, 2003) to DGVMs. Statistical species distribution model can be fitted for many species but do not directly represent the complex relationships between climate and plants such as competition, carbon dynamics, nutrient cycling

(Pearson and Dawson, 2003) and they typically ignore CO_2. On the other hand DGVMs, as discussed in Section 5, represent the key ecophysiological processes of plant growth and competition as a function of environmental conditions. Yet, most of the regional models have several caveats and limitations. The first limitation is that many DGVMs typically use bioclimatic limits (Haxeltine and Prentice, 1996) to constrain the climatic niche where modelled PFTs can grow (e.g. BIOME3 (Haxeltine and Prentice, 1996) or LPJ (Sitch et al., 2003)). For example, Sitch et al. (2003) assume different temperature limits for survival and establishment of PFTs. However, it has been argued that this may imply that areas will be projected as climatically unsuitable for particular PFTs, although in reality they could be tolerable, or vice versa (Reu et al., 2014). Climate envelopes in DGVMs were derived from contemporary distribution and patterns of PFTs and might not be valid when projecting vegetation into the future (Scheiter et al., 2013). One reason is that temperature thresholds might be influenced by elevated atmospheric CO_2 concentration (Ehleringer et al., 1997). Elevated CO_2 increases water use efficiency (WUE) or the photosynthetic efficiency and will likely modify bioclimatic limits as well as biome boundaries in climate space (Franks et al., 2012).

Second, DGVM simulation results are at the same resolution as input data. Therefore, DGVMs are often limited by the coarse spatial and temporal resolution of data available for model input and parameterization. Most DGVMs are deterministic in the sense that they simulate similar biome types for similar climate conditions and similar model initialization. When conducting model simulations with coarse resolution environmental data, vegetation is homogenous within areas with similar climate, e.g. within a grid cell of 1°. Vegetation heterogeneity within the grid cell cannot be resolved (but note that tiling schemes are often applied to account for areas used for land use or covered by water and human settlements). Therefore, higher resolution data for climate, soil as well as topography and consideration of associated processes such as water balance, radiation and seed dispersal are required (Moorcroft et al., 2001). High resolution climate data can be derived from regional

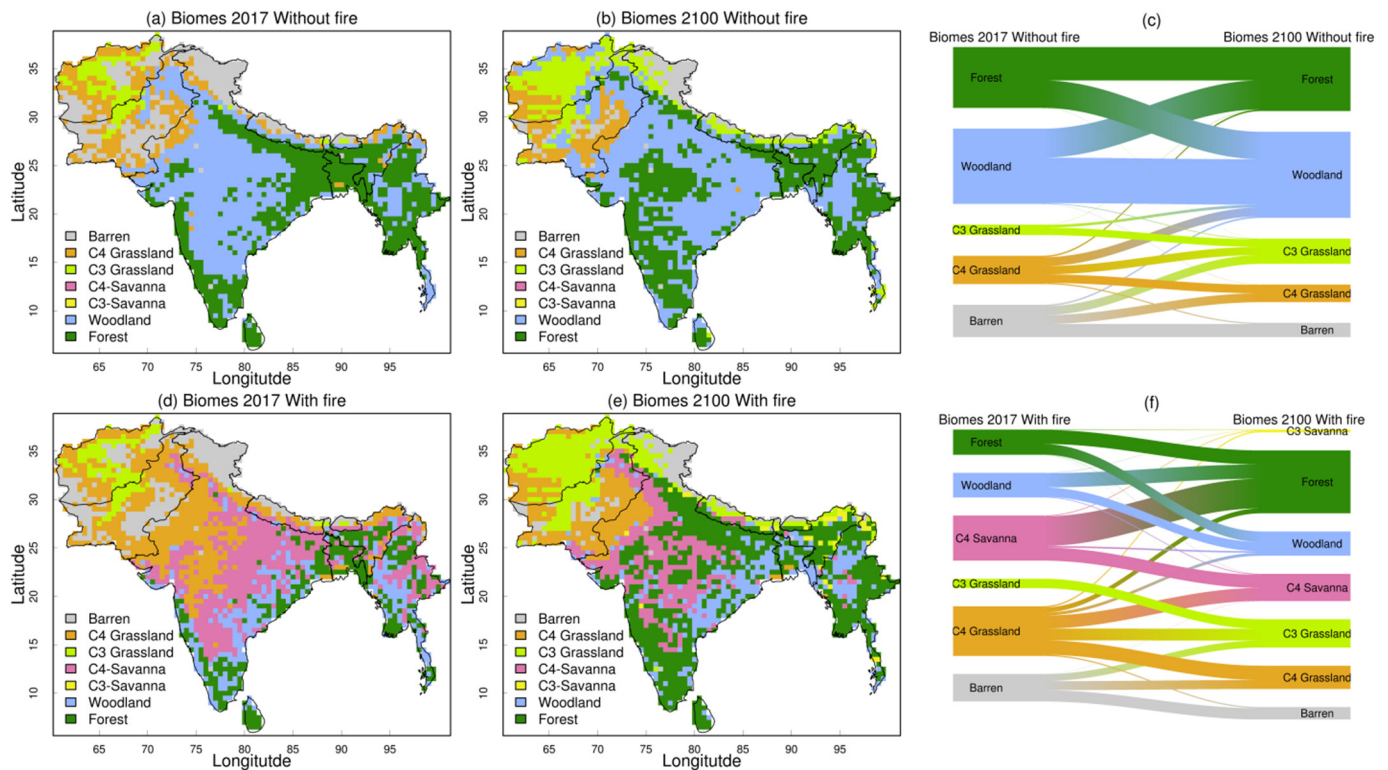**Fig. 2.** Biomes simulated by aDGVM (Scheiter et al., 2012; Scheiter and Higgins, 2009) without fire (a and b) and with fire (d and e) for the years 2017 (a and d) and 2100 (b and e). Sankey graphs show the biome shifts from 2017 to 2100 (c) without fire and (f) with fire. Under both scenarios, biomes are sensitive to climate change and biome shifts occurred. For the biome classification scheme see Scheiter et al. (2012).

climate models (RCMs, Feser et al., 2011; Rummukainen, 2010). While these models can capture important climate phenomena of a region such as monsoons or extreme events, model runs are typically computationally expensive such that high resolution data is only available for small regions (Valdes et al., 2017). Alternatively, high resolution data can be obtained from statistical interpolation methods (Fick and Hijmans, 2017). The disadvantage of this approach is that interpolated climate data often ignore important local climate phenomena (Hijmans et al., 2005) and they often provide climatologies instead of continuous time series.

Third, there are only few DGVMs studies for South Asia, most of which were conducted with the BIOME model (versions 3 and 4, Ravindranath et al., 2006; Ravindranath and Sukumar, 1998, 1996). The BIOME model has a very simple representation of plant physiology in the context of Indian ecosystems (Ravindranath et al., 2006; Ravindranath and Sukumar, 1998).

Fourth, how vegetation was traditionally represented in many DGVMs has recently received much criticism (Pavlick et al., 2013; Van Bodegom et al., 2012; Scheiter et al., 2013). Models did not satisfactorily represent the variability in vegetation responses to the environment as observed in nature, hindering representations of vegetation-climate interactions and very likely biasing estimates of carbon budgets (Verheijen, 2015). In traditional DGVMs (e.g. LPJ (Sitch et al., 2003), SDGVM (Woodward and Lomas, 2004) or ORCHIDEE (Krinner et al., 2005)), only a limited number of vegetation types are used to represent the vast number of plant species and their responses to the environment.

Fifth, soil is the largest terrestrial pool of organic carbon (Jobbágy and Jackson, 2000; Tarnocai et al., 2009) and soil respiration plays a significant role. Soil respiration varies among different vegetation types which could be well explained by the soil conditions (Huntingford et al., 2017; Wang et al., 2013). Vegetation, depending on its characteristics (e.g., C_3 or C_4, evergreen or deciduous, trees or grasses) and climate control soil moisture (Arora, 2002) and soil temperature and thereby soil heterotopic respiration (Jenkins and Adams, 2010). For example, bamboos (Xu et al., 2013) and mangroves (Alongi, 2012; Donato et al., 2012) constitute a significant component of South Asian biomes and are capable of high rates of carbon sequestration in the tropics (Donato et al., 2011). Lianas, bamboo or succulents not only have different effects on carbon cycling but they also serve as habitat for different animal communities.

To understand cascading effects on biodiversity at different trophic levels and biotic interactions, we need to understand processes in different biomes in terms of diversity, vegetation structure, ecosystem services. Therefore, for the representation of vegetation and diversity, when we look at regional scale rather than at global scale, we need more diversity in models if we are to understand climate change impacts on diversity at various trophic levels. Given these caveats, we suggest that DGVMs should reflect real-world processes with more detailed vegetation types (more PFTs) or more flexible FT approaches to better represent diversity and the carbon cycle in ecosystems (Frasson et al., 2015; Harper et al., 2018, 2016).

8. Potential of developing DGVMs for South Asia

Numerous vegetation types and growth forms are characteristic of South Asia's flora, some of which are not represented in state of the art DGVMs. For example, tropical dry deciduous and wet deciduous forests are typically represented as tropical deciduous forest even though they represent distinct vegetation types differing in productivity and their response to environmental resources. Lavorel et al. (2007) found that DGVMs using fewer than 13 PFTs might be unable to simulate fine scale vegetation patterns, and simulate abrupt changes in vegetation along environmental gradients instead of smooth transitions that are more common in nature (Quillet et al., 2010). Table 1 lists South Asian biomes, biome-specific growth forms (Ramankutty et al., 2010,

Table 1
Biomes, growth forms and processes relevant for modeling South Asia's vegetation. We argue that including these key growth forms (within a PFT or a FT approach) and processes into dynamic global vegetation models (DGVMs) will allow us to better represent the biome distributions and biome boundaries of South Asia, as well as climate change and land use change impacts on vegetation.

Biome	Growth form	Processes
Evergreen forest	Dry forest tree	Water competition
	Wet forest tree	Light availability
	Dry montane temperate tree	Cold tolerance
	Moist montane temperate tree	Photoperiod
	Lianas	Phenology
	Bamboos	
Deciduous forest	Dry forest tree	Light availability
	Wet forests tree	Water competition
	Lianas	Phenology
Savanna	C_4 grass[a]	Surface fire
	Fire tolerant tree[b]	
Shrubland	C_4 grass[a]	Water competition
	Shrub[a]	Fire
Grassland	Annual C_4 and C_3 grass	Frost
	Perennial C_4 and C_3 grass	Water availability
Thicket/thorny forest	Shrub[a]	Water availability
	C_4 grass[a]	
	Succulent tree	CAM photosynthesis
Mangroves	Mangrove tree	Saline water
		Viviparous germination

[a] Included in existing DGVMs.
[b] Included in aDGVM (Scheiter et al., 2012) and ED2 (Trugman et al., 2018).

Fig. 1a, b) and processes that are relevant for modeling each of these biomes. In the following sections, we describe vegetation types and growth forms and suggest how they can be incorporated into DGVMs to allow more reliable projections of past, present and future vegetation dynamics in South Asia.

8.1. Tropical deciduous forest

Tropical deciduous forests cover the major portion of South Asia's forested area and comprise both dry and moist deciduous forest (Fig. 1a, b). These forests are found in southern India (Deccan region), Western Himalayas, Myanmar and along the Western Ghats (Reddy et al., 2015). Tropical dry deciduous forests occupy 34.80% and tropical moist deciduous forests occupy 33.19% of the total forest cover in India (Reddy et al., 2015). Both forest types are generally represented by a single PFT in DGVMs (typically by "tropical broad-leafed raingreen trees"). Yet, dry and moist deciduous forests have different successional strategies in response to water and light availability (Lohbeck et al., 2015).

Dry forest species have greater drought survival rates due to higher stem hydraulic conductance, higher capacity for CO_2 assimilation (Brenes-Arguedas et al., 2013), higher stem density and tough, thick tissues with high cell survival at low water content (Kursar et al., 2009). They have thicker and deeper tap roots which are associated with drought tolerance. Despite their higher photosynthetic capacity, these species are shade-intolerant with lower growth rates in the shady understory, probably because of higher maintenance costs of the root systems (Brenes-Arguedas et al., 2013). Moist forest species have lower photosynthetic capacity and higher leaf area ratio to capture light efficiently in shady forests (Brenes-Arguedas et al., 2013). Deeper and thinner roots allow for resource acquisition in poor soils (Poorter and Markesteijn, 2008). These traits characterize shade-tolerant species and explain high growth rates of moist forest species in the shady understory of forest.

In most DGVMs, plant water stress is driven by external factors, such as precipitation, humidity and soil type and texture (Xu et al., 2016). However, a more realistic approach would be to describe plant water stress through whole plant hydraulic strategies and functions of water pressures within the plant vascular system, defined via water potential

in leaf, stem, branches and soil (Matheny et al., 2017). A decline in leaf water potential can reduce photosynthesis in tropical dry forest (Brodribb et al., 2002) and other ecosystems (Manzoni, 2014; Xu and Baldocchi, 2003), and trigger leaf shedding if leaf turgor cannot be maintained (Sobrado, 1993). Leaf water potential is also influenced by leaf, stem and root hydraulic traits (Cochard et al., 2002). Interspecific hydraulic trait variation allows plants in similar environments to display different phenological and photosynthetic responses to water stress (Méndez-Alonzo et al., 2013; Poorter and Markesteijn, 2008). The coordination of various hydraulic traits in different plant tissues (Markesteijn et al., 2011; Méndez-Alonzo et al., 2012; Zhu et al., 2013) possibly explains the phenology of deciduous trees because natural selection favors efficient water transport along hydraulic pathways (Hickler et al., 2006; Langan et al., 2017).

Dry and moist deciduous trees could be integrated into DGVMs by including traits associated with plant hydraulics, drought tolerance and phenology. Most existing DGVMs use a formulation based on Darcy's law to describe water transfer through the soil-plant-atmosphere continuum. This approach assumes that water transfer is controlled by a plant's hydraulic conductivity and the gradient between the hydraulic potential of soil and plant (Christoffersen et al., 2016; Gentine et al., 2016; Roman et al., 2015). This approach has been effective for simulating how drought affects tropical forests at large scales (Xu et al., 2016), yet, it mostly ignores factors affecting xylem capacitance and conductance (Sperry et al., 1998) and is incapable of simulating water storage capacity of plant biomass (Matheny et al., 2017; Santiago et al., 2017). This limitation can be addressed by modeling dynamic changes in xylem capacitance as a function of xylem water potential by assuming a relationship between the water stored in the plant and the water potential of the water stored in plant biomass (Huang et al., 2017; Mirfenderesgi et al., 2019).

8.2. Tropical evergreen forest

Tropical evergreen forest is found in the Northeast of India, Western Ghats, Tamil Nadu coast, Lakshadweep, Andaman and Nicobar, Bangladesh, Myanmar and the lower foothills of Nepal (Fig. 1a, b). Indian tropical evergreen forests are divided into wet and dry evergreen forest (Joshi et al., 2006; Reddy et al., 2015). Dry evergreen forests receive less rainfall (<2000 mm) than wet evergreen forests (>2000 mm, Mani and Parthasarathy, 2006). Tropical dry evergreen forests occur as patches and they are short-statured and largely three-layered with a sparse and patchy understory flora (Venkateswaran and Parthasarathy, 2005). Yet, structure and physiognomy of dry evergreen forest varies in different climatic regimes (Blasco et al., 2000). Tree inventories for tropical dry evergreen forests show large differences in density and basal area, probably due to different geographical location and varying annual rainfall patterns (Mani and Parthasarathy, 2006). The spatial heterogeneity of climatic conditions on the western coast of southern peninsular India supports tropical dry evergreen forest (Champion and Seth, 1968). They are further distributed on the eastern (Coromandel) coast of India and extending about 50 km inland, northern Sri Lanka (Blasco and Legris, 1973), northeastern Thailand (Bunyavejchewin, 1999) and southwest China (Hongmao et al., 2002). Wet evergreen forests are dominated by broad-leaved evergreen trees growing taller than 30 m in height whereas trees in dry evergreen forest are typically 9 to 12 m tall (Daniels et al., 2007).

Most DGVMs do not explicitly represent the differences between dry and wet evergreen forest and represent both forest types by a single PFT ("tropical broad-leaved evergreen tree"). We suggest to include two distinct PFTs to describe wet and dry evergreen forest types in DGVMs. This could be achieved by including traits associated with phenology, distinct tree architecture, resource allocation and competition for water and light, analogously to the tropical deciduous forest (see Section 8.1). Trees in dry evergreen forest are water limited and have different allocation and phenology schemes than trees in wet evergreen

forests (Borchert, 1994; Hasselquist et al., 2010; Reich, 1995). These differences could serve to simulate forest with different height structure and type. A better representation of seasonality of water availability, plant structure and plant hydraulics (see Section 8.1) along with phenology could enhance the performance of DGVMs in the unique tropical evergreen forest biome in the South Asia.

8.3. Temperate montane forests

Temperate montane forests are found in the Himalayas at altitudes ranging from 1800 to 4000 m where humidity and temperature are low (Reddy et al., 2015). Himalayan ecosystems are projected to be extremely sensitive to future climate change (Chaturvedi et al., 2011). Temperate forest has been broadly classified into moist temperate and dry temperate forest (Joshi et al., 2006; Reddy et al., 2015). In Himalayan moist temperate forest, annual rainfall varies from 1500 mm to 2500 mm. These forests are dominated by *Quercus*, *Pinus* and *Juniperus* species that can grow up to 45 m tall. On the other hand, Himalayan dry temperate forests are dominated by Rhododendron species and are found in a narrow belt between 3000 and 4000 m in the western Himalayas. Due to the high elevation, the Himalayan region experiences alpine and tundra like climate which is suitable for sub-alpine forests. Sub-alpine forests are found throughout the Himalayas from Ladakh in the west to Arunachal Pradesh in the east at the altitude from 2800 m to 3800 m. These forests receive <650 mm mean annual precipitation. Epiphytic mosses and lichens are abundant in these forests.

Generally, DGVMs represent these forests by either the 'temperate needle-leaved tree' PFT or the 'temperate broad-leaved tree' PFT, while neglecting the heterogeneity of Himalayan temperate forest which is related to heterogeneity in topography and climate. In cold-adapted plants, temperature is a key driver of the resumption of tree activity in spring, although temperature effects vary among organs (Delpierre et al., 2016). Temperate species are tolerant to extremely low temperatures (Strimbeck et al., 2015); they prevent cavitation by higher hydraulic resistance of the soil-plant continuum (Cochard et al., 2009). Low temperature inhibits investment of carbon into structural growth for a substantial fraction of the growing season (Körner, 2003). Temperate species usually have higher leaf nitrogen, leaf mass per unit area, photosynthetic assimilation and respiration rates as compared to tropical species (Xiang et al., 2013). In addition, environmental factors such as the length of the photoperiod and water stress play an important role in shaping phenology of all tree organs (leaves and reproductive structures, wood, roots, reserve compounds) in the temperate zones (Delpierre et al., 2016). Our knowledge on temperature dependence of carbon allocation, hydraulic conductivity, phenology along with the dependence of root growth and mortality on soil temperature and moisture should be incorporated into DGVMs (Delpierre et al., 2016).

Current DGVMs often use bioclimatic limits to separate temperate vegetation from tropical and boreal vegetation. We suggest to represent these cold-adapted vegetation types using traits related to their ecophysiology and cold adapting strategies such as resistance to freeze induced embolism or different carbon allocation strategies which would evolve according to the environmental conditions.

8.4. Thickets and thorny forest

Thickets and thorny forests are open forests dominated by thorny, hardwood species. They are mostly found in arid regions in the North-West of South Asia extending into Pakistan and Deccan where mean annual rainfall is <700 mm. Acacias, palms, euphorbias and invasive cacti (Novoa et al., 2015) are common in these areas. Trees are scattered, do not grow beyond 10 m and have deep roots in order to access moisture in deep soil layers (Pierret et al., 2016; Schenk and Jackson, 2005, 2002; Shankarnarayan et al., 1987). Many tree species in this biome are fine leaved which is primarily an adaptation to avoid overheating

(Wright et al., 2017). Fine-leaved species evolved to maximize plant performance in harsh conditions (Wright et al., 2017). Under water limited conditions, leaves evolved into thorns and spines which minimizes the transpiration (Givnish, 1979) and serves as protection against herbivory. Due to sufficient solar radiation in these dry and open habitats, fine leaves are sufficient for carbon assimilation and a positive carbon balance of these plants.

In arid regions, plants further adapted to the prevailing dry and hot climate and to frequent drought by evolving succulence. Succulent plants conserve water in stems, and most of these plants fix CO_2 through the crassulacean acid metabolism (CAM) photosynthetic pathway (Holtum et al., 2017). Succulents are adapted to arid conditions of Western and Deccan regions of South Asia. Most DGVMs do not represent succulents, and thickets and thorny forests are represented as tropical deciduous forest functional type. In reality, these forest types differ strongly in structure, phenology and function. For a better representation of this biome in DGVMs, we suggest that resource allocation strategies of plants should be adapted to allow carbon allocation into thorns for protection against grazing and roots to access deeper soil water. The costs or tradeoffs of this allocation strategy should be explicitly modelled. We also suggest to model the partitioning of above and below ground biomass with an adaptive allocation model in such a way that thorny trees could be differentiated structurally from forest trees.

Wright et al. (2017) showed that leaf size follows the temperature distribution. This relation could be used to distinguish between broad and fine leaved PFTs in DGVMs and to better represent leaf energy balance in different climate settings. Succulents could be implemented by adding a water storage pool that is filled when water is available and used in dry periods. CAM plants make up almost 50% of plant biomass in arid and semi-arid regions of the world (Syvertsen et al., 1976). CAM plants are able to fix CO_2 in organic acids in the mesophyll chlorenchyma during the dark and then utilize the CO_2 for the formation of carbohydrates via the C_3 pathway during the light period (Hartzell et al., 2018). The environmental variability at the daily and weekly timescale is an important factor in CAM functioning (Hartzell et al., 2015) and should be considered in models. Physiological models of CAM have already been introduced (see e.g. Bartlett et al., 2014; Owen and Griffiths, 2013) and implemented in some models (Hartzell et al., 2018). Yet due to their complexity, CAM models have not been widely adopted and most DGVMs are confined to the C_3 and C_4 pathways. We conclude that fine leaved PFTs, succulence and the CAM photosynthetic pathway should be implemented in DGVMs as these features are important components of dryland and tropical ecosystems.

8.5. Savanna

Savannas are mixed tree-grass systems characterized by a discontinuous tree layer in a continuous grass layer (House et al., 2003; Scholes and Archer, 1997). Savannas are often maintained through herbivory and frequent burning which lead to the formation of savanna mosaics. In addition, the ecosystem state depends on age and origin of the ecosystem (Moncrieff et al., 2014), and the intensity of biotic disturbance. Small differences in soil, topography and climate can determine whether savanna or dry forest occurs in a particular area (Prance, 2006). It has been argued that savannas in South America (Langan et al., 2017; Wuyts et al., 2017) and Africa (Favier et al., 2012; Higgins and Scheiter, 2012; Scheiter and Higgins, 2009) are bi-stable, that is, vegetation is in a savanna state in the presence of fire while environmental conditions would allow a forest state. aDGVM model simulations indicate vast bi-stable area in South Asia (Fig. 3). Simulations with fire show large extent of savannas (Fig. 2d, e), whereas in the absence of fire, savanna regions are occupied by forest, woodland or grassland (Fig. 2a, b).

South Asian savannas are often misinterpreted as degraded forests although most of these savanna systems are ancient (Ratnam et al.,

2016). Large areas in South India and on the Deccan plateau classified as tropical dry forest comprise fire-resistant savanna tree species, an understory dominated by shade-intolerant C_4 grasses and they require fire to maintain grass-tree co-existence. Hence, these ecosystems should be classified as mesic savannas (Ratnam et al., 2011).

Savanna tree species in fire-prone environments are highly fire tolerant and generally recover rapidly after fire (Bond and Midgley, 2001; Hoffmann et al., 2004; Schutz et al., 2009). They invest more resources to root and underground storage, to seed establishment and to resprouting than forest tree species (Hoffmann et al., 2003; Ratnam et al., 2011; Schutz et al., 2009; Simon et al., 2009; Wigley et al., 2009). Saplings of savanna trees grow rapidly in height in order to escape the flame zone (Higgins et al., 2000; Wigley et al., 2009). Surface fires consume grass biomass and small saplings whereas tall trees are not damaged by fire (Bond, 2008; Hoffmann et al., 2012; Williams et al., 1999). Many savanna species have a high bark growth rate and thick bark. These traits protect the inner cambium and minimize fire damage (Champion and Seth, 1968; Charles-Dominique et al., 2017; Gignoux et al., 1997; Hoffmann et al., 2009, 2003). These features result in very low fire related mortality in adult savanna trees.

A distinction between forest and savanna trees is ignored in many DGVMs (for exceptions see Baudena et al., 2015; Scheiter et al., 2012 and Trugman et al., 2018). Fire tolerance traits and adaptations of savanna trees to fire, in particular resprouting from apical bud after fire (Burrows, 2002; Williams, 2009) and differential effects on small and tall trees (demographic bottlenecks, Higgins et al., 2000) should be included in DGVMs to enhance model performance in the savanna biome of South Asia. Scheiter et al. (2012) showed that the presence of a savanna tree type extends the area covered by savannas in Africa, compared to a model without the savanna tree type. Trugman et al. (2018) showed that tropical vegetation dynamics depend not only on rainfall and changing fire frequencies but also on fire survival strategies of trees. Fire survival strategy is also important in regulating tree demography in ecosystems exposed to fire, which facilitates coexistence of different plant functional groups in tropical savannas.

8.6. Shrubland

Shrubs form an important component of various vegetation formations in South Asia. Shrublands are found in the semi-arid regions, especially in Afghanistan, Pakistan, the western and southern part of India. The distribution of rainfall patterns seems to be the most important factor in maintaining shrub cover, although shrublands occupy different geological formations and soil types (Dakshini, 1989).

Shrubs are semi-woody (Götmark et al., 2016) multi-stemmed plants with branches rising from the base, growing up to 3 to 4 m in height (Götmark et al., 2016; Zizka et al., 2014). They can be either evergreen or deciduous and woody vegetation cover is typically <10% in shrub dominated ecosystems.

For a given biomass, shrubs have higher sapwood area and higher hydraulic conductivity than trees due to relatively larger total stem cross-section area (Götmark et al., 2016). These features imply a competitive advantage of shrubs under more arid and water-limited conditions. Shrubs can cope with fire (Clemente et al., 1996) due to their ability to re-sprout efficiently after being damaged by fire (Hoffmann and Solbrig, 2003). Mature trees typically grow taller than shrubs due to their single-stemmed architecture (Zizka et al., 2014), giving trees a competitive advantage in dense ecosystems where light is limiting. In addition, tall trees have an advantage in fire-driven ecosystems, once they grow tall enough to avoid fire damage of leaves (Hoffmann et al., 2012).

DGVMs often ignore the multi-stemmed architecture of shrubs and treat them as trees with adjusted architecture and hydraulic properties (Gaillard et al., 2018). The implementation of shrubs in DGVMs requires a better representation of the multi-stemmed architecture, fire response, hydraulic conductivity and water competition as well as the
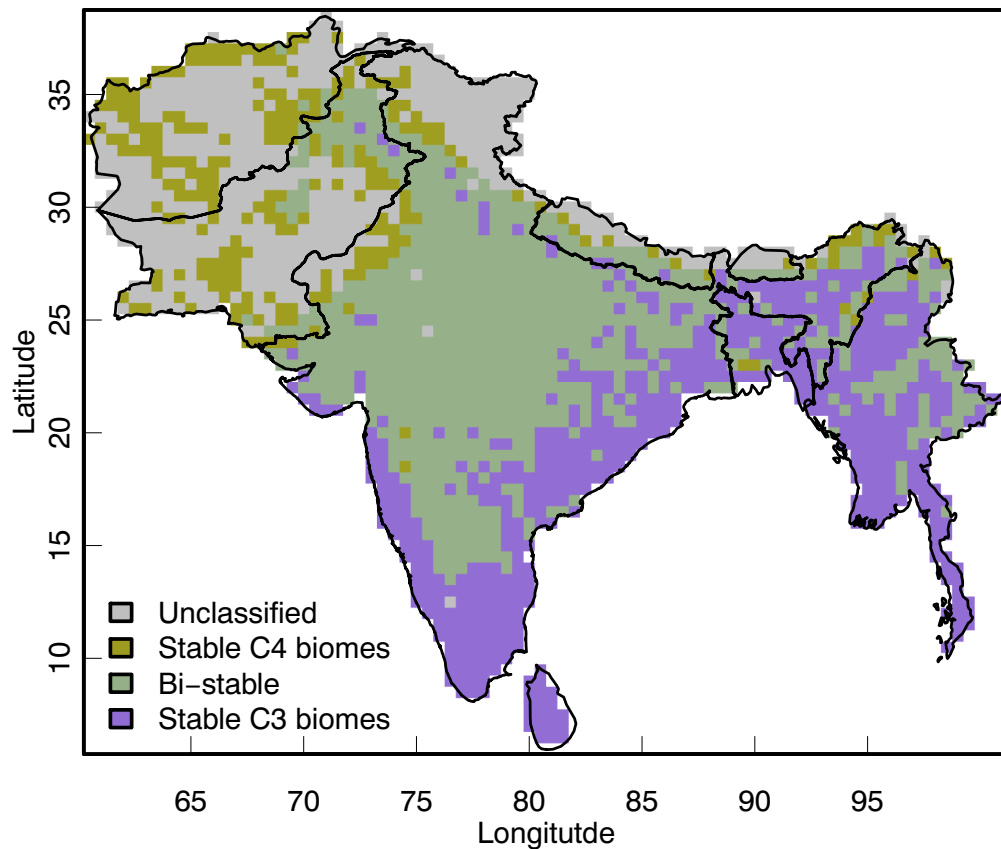
Fig. 3. Bi-stability between C$_4$ dominated biomes (savanna and C$_4$ grassland) and C$_3$ dominated biomes (forest and woodland) simulated by aDGVM (see Fig. 1a, e). Vegetation in a grid cell is bi-stable if it is in a C$_4$ biome state in the presence of fire but in a C$_3$ biome state in the absence of fire.

emerging trade-offs between shrub and tree growth form. In Gaillard et al. (2018), we integrated shrubs into the recent version of aDGVM2 by explicitly considering their multi-stemmed architecture. We showed that the ability to model shrubs and trees as distinct growth forms improves our understanding of the current distribution of ecosystems with a substantial component of shrubs (Gaillard et al., 2018). The shrub implementation in aDGVM2 was developed for Africa (Gaillard et al., 2018) but preliminary results show that aDGVM2 can simulate shrub dominated areas in the North-West of India (Kumar et al., unpublished). Shrub encroachment is a major concern in Indian savannas but also in savannas globally (Stevens et al., 2017) and the model will allow us to understand past and future shrub encroachment.

8.7. Grassland

Grasslands occupy nearly 24% of the area of South Asia in several biogeographical regions. They consist of a community in which grasses predominate, along with forbs as co-dominants and exhibit a wide range of ecological characteristics (Singh et al., 1983). Woody plants are either absent or present in low densities. Grasslands dominate in the areas of low to moderate annual precipitation, drought, extreme temperature fluctuations, relatively shallow soil, fire and grazing (White et al., 2000). In South Asia, grasslands are mostly dominated by C$_4$ grass species in the tropical regions (Indian peninsular and montane areas in the Western Ghats and Himalayas) and by C$_3$ grass species in the temperate regions (Northwest of Pakistan). Except montane grasslands of the Himalaya and the Western Ghats, grasslands in India are anthropogenic in origin and evolved under the influence of fire, livestock grazing, clearing forest, flood, drought (Bor, 1960; Singh et al., 1983) and inherent properties of soil (Kotwal and Pande, 1980; Pandey et al., 1985). The extent of grassland is prone to human expansion, heavy infestation by

unpalatable and thorny alien invasive plants, soil erosion and compaction. A need for an assessment of grass cover and long term ecological studies on various grasslands in India was already expressed in the 1970s (Dadadghao and Shankarnarayan, 1973; Yadava and Singh, 1977).

Most DGVMs simulate only two PFTs representing entire C$_3$ and C$_4$ herbaceous communities including grasses, forbs and other herbaceous species. An explicit representation of seasonal, annual and perennial grasslands found in South Asia is missing. The boundary between C$_3$ and C$_4$ grasslands is typically defined by bioclimatic limits while underlying processes defining the boundary are not explicitly considered. This approach is particularly critical under pre-industrial or elevated CO$_2$ concentration because it has been shown that the relative dominance of C$_3$ and C$_4$ grasses is related to temperature and CO$_2$ and not only defined by a bioclimatic limit based on temperature (Ehleringer et al., 1997). In addition, C$_3$ and C$_4$ grasses may coexist while the utilization of bioclimatic limits implies that an area is dominated by C$_3$ or C$_4$ grasses. Different types of grasslands with different height structure, water requirement and demography should be represented in more details in DGVMs. We suggest that a better representation of reproductive strategies (Pfeiffer et al., 2019), water competition, light competition, fire seasonality and soil properties should enhance the performance of DGVMs to simulate grasslands in South Asia.

8.8. Mangroves

Mangroves are characteristic intertidal plant communities of sheltered subtropical and tropical coastlines (Saenger, 2002). In South Asia, mangroves are mainly found in the river deltas along the east coast and west coast of peninsular India and coastal regions of Sri Lanka (Fig. 1b). During the last century, 40% of the mangrove areas

were lost (Kumar, 2000) and they are considered vulnerable to climate change (Berger et al., 2008). Coastal processes in different geomorphological settings (e.g. inundated coastal area) along with natural disturbances (e.g., hurricanes) define the structural complexity of mangrove forests, including maximum stand height and tree morphology (Doyle et al., 1995; Doyle and Girod, 1997; Duke, 2001). Mangrove tree species are halophytic evergreen and have pneumatophores/stilt roots and viviparous germination, i.e. the seeds germinate while still on the mother trees.

Field studies have reported that various factors such as regulators (pH, salinity), resources (light, nutrient, space), and hydroperiod (frequency and period of inundation) control mangrove structure and function (Huston and Huston, 1994). Water salinity is a critical regulator influencing the structure of mangrove forests (Ball, 2002; Castañeda-Moya et al., 2013, 2006). Nutrients such as nitrogen and phosphorus are key resources that define growth and spatial distribution patterns (Kristensen et al., 2008). The processes governing mangrove response to hydroperiod, light, nutrients, salinity and other soil conditions need to be explored (Berger et al., 2008).

Mangroves are usually not represented explicitly in DGVMs. Yet, several models have been developed independently to understand the dynamics of mangrove ecosystems and to provide capability to forecast their vegetation dynamics under different management scenarios and natural disturbance regimes. Some of these models are individual-based models (IBMs) such as FORMAN and KIWI and address forest stand dynamics whereas MANGRO focuses on landscape dynamics (Berger and Hildenbrandt, 2000; Chen and Twilley, 1998; Doyle et al., 2003, 1995).

DGVMs should integrate mangroves explicitly to describe the essential processes of trees linked to resource, regulator and hydroperiod gradients, and test their relative importance in controlling mangrove forest dynamics. DGVMs coupled with explicit mangrove models would support research related to coastal protection and sustainable use of South Asia's coastal ecosystems. The individual-based approach of existing mangrove models would facilitate the inclusion into individual-based DGVMs.

8.9. Lianas

Lianas are woody vines that start growing as independent life form but subsequently depend on other plants (trees) to reach the forest canopy (Letcher and Chazdon, 2009; Vivek and Parthasarathy, 2015). In South Asia, lianas are found in the tropical dry evergreen forests at the Coromandel Coast and in the Eastern Ghats (Parthasarathy et al., 2008) and Sri Lanka. Lianas play a major role in tropical forest dynamics (Putz, 1984; Schnitzer et al., 2000) by competing with trees for both aboveground and belowground resources (Schnitzer and Bongers, 2002), resulting in reduced recruitment, regeneration, growth and survival of trees (Ingwell et al., 2010; Schnitzer and Carson, 2010). Although lianas and trees are woody plants, both growth forms differ from trees in their functional traits including climbing mechanism (Holbrook and Putz, 1996) and light requirements (Gianoli et al., 2010). Abundance, species diversity and distribution of lianas are explained by abiotic and biotic factors, such as total rainfall, rainfall seasonality, soil fertility, forest canopy structure and disturbance regimes (Addo-Fordjour et al., 2012; Schnitzer et al., 2005). The majority of lianas is brevi-deciduous or deciduous, whereas 50% of the host trees are evergreen (Vivek and Parthasarathy, 2015). This reflects the distinctive vegetative traits and leafing phenology of tree and liana life forms in the same ecosystem. Leaf size of lianas varies from microphyllous to mesophyll. Smaller leaves can maintain favorable leaf temperature and greater photosynthetic water-use efficiency under low water availability and high solar radiation (Muthumperumal and Parthasarathy, 2010). It has been argued that the prevalence of microphyllous leaves is a functional strategy adopted by lianas in tropical dry evergreen forest, which experiences 6 to 8 months of dry period. In recent years,

the tropical dry evergreen forests on the Coromandel Coast experienced anthropogenic pressure, resulting in modified tree height (Baithalu et al., 2012). These changes in host plants are likely to affect lianas depending on trees for their physical support.

We argue that lianas should be included in DGVMs as structurally distinct life form for a better representation of tropical forest dynamics where both lianas and trees compete for same resources (Schnitzer et al., 2005). Lianas have a competitive advantage over trees with respect to accessibility of water and light. The effects of increasing liana abundance and biomass would alter the carbon cycle and carbon balance of tropical forests by reducing forest-level carbon storage and sequestration (Heijden et al., 2013; Phillips et al., 2002; Verbeeck and Kearsley, 2016). Including lianas in DGVMs would help to better understand the dynamics of South Asia's dry evergreen forest and potential impact of future climate change. As woody plants are already implemented in DGVMs, inclusion of lianas would primarily require modeling of the interactions between trees and lianas (Verbeeck and Kearsley, 2016).

8.10. Bamboos

Bamboos belong to the subfamily *Bambusoideae* in the family *Gramineae*, and have about 1500 known species worldwide (Li and Kobayashi, 2004). In India, bamboo forests cover about 14 million ha of land, with 125 indigenous and 11 exotic bamboo species (FSI, 2011). Bamboos are widely distributed in temperate and tropical regions of South Asia (Sharma, 1980). Dwarf herbaceous species (*Sasa kurilensis*) of bamboo are found in temperate regions and giant species (*Dendrocalamus membranaceus, Melocanna baccifera*) that can grow up to 20 m tall in tropical regions (Bystriakova et al., 2004). It is one of the fastest growing plants with a daily growth rate of 30 to 120 cm. The maximum height of between 5 and 20 m is reached in a single growing season of between 2 and 4 month length (He et al., 2014). Bamboos are an important carbon sink and have high carbon sequestration potential. However, their response to climate change is still poorly understood (Xu et al., 2013).

Bamboos have a unique phenology which controls resource allocation between mature individuals and young recruits via underground rhizomes (Song et al., 2016). Individual plant phenology affects the functioning of bamboo forest ecosystems (Mao et al., 2016). Warmer temperatures with longer periods of direct sunlight during the cloudy growing season increase resource accumulation within culms leading to high recruitment (Qin et al., 1993). Light availability affects the variation in culm size and bamboo stand density (Reid and Jinchu, 1991; Taylor and Zisheng, 1988). During the recruitment period, non-structural carbon (NSC) of the leaves, branches, trunks and rhizomes of attached mature bamboos is re-allocated to the fast growing shoots of young recruits via underground rhizomes. The allocation of NSC to young recruits stops when the leaves of the young bamboos can assimilate enough carbohydrates (photoassimilates) to meet the plant's carbon demand (Fu, 2001). This periodicity is mainly due to the unique strategy of bamboo growth and reproduction, the integral structure of the culms-rhizome system and soil nutrients (Mao et al., 2016).

Bamboos are susceptible to fire damage but are capable of rapid clonal growth that gives an advantage in post fire environments. It can quickly occupy the open space created by fire and monopolize its resources (Gagnon and Platt, 2008), allowing intense competition with tree recruits. Once fully gown, the bamboo canopy can limit light penetration to the forest floor (Montti et al., 2011), and suppress germination, regeneration and recruitment of tree seedlings (Budke et al., 2010; Montti et al., 2011). Fire intensity and frequency can affect clump regeneration, production and development in forest communities (Kachina et al., 2017; Smith and Nelson, 2011).

Including bamboos into DGVMs can help to understand interactions between bamboo and tree regeneration in post fire environments as well as under future climate change in South Asia. We argue that the

implementation of specific carbon allocation schemes and phenology of bamboos along with its unique recruitment cycle in DGVMs would enhance the model's capabilities in simulating bamboo-dominated ecosystem. Bamboos are important for carbon sequestration in tropical ecosystem and have high economic value.

9. A way forward toward next-generation DGVMs

The complexity of vegetation dynamics makes it challenging to simulate the influence of climate on vegetation and on processes such as carbon assimilation, allocation and release, soil carbon dynamics and competition. Many of these ecological processes still remain uncertain and need to be further analyzed, both by empirical and by modeling studies (Pavlick et al., 2013; Van Bodegom et al., 2012). Special attention should be given to the representation and parameterization of PFTs or traits in FT approaches in DGVMs along with accurate benchmarking of predicted patterns of vegetation distribution in tropical ecosystems. Another major issue in vegetation modeling is the incorporation of disturbances (i.e., fire and drought) and a better description of the land cover (in particular land use and non-vegetated surfaces). Some of these disturbances are included in global scale studies but land use needs to be explicitly represented at regional or even site scale. Including disturbances in DGVMs is expected to improve simulation results, thereby increasing the agreement between simulations and observations (Felzer et al., 2007; Ashmore, 2005).

In order to improve the representation of vegetation in DGVMs, trait variability can be incorporated into DGVMs in two different ways (Wullschleger et al., 2014). The first approach would be to vary parameters of PFTs as a function of environmental variables. Plant community mean trait values are directly related to environmental conditions resulting in trait convergence for the PFT. This approach of trait-environment relationships has shown consistent patterns relating leaf functional traits to climate (Wright et al., 2005), soil fertility (Ordoñez et al., 2009) or both (Ordonez et al., 2009; van Ommen Kloeke et al., 2012). Incorporation of trait-environment relationships into JSBACH indicated major consequences of trait variability on vegetation and carbon dynamics for the current climate (Verheijen et al., 2013). It resulted in a productivity difference of up to 50% in the tropics and 35% change in dominant vegetation cover compared to simulations with fixed traits. Simulated vegetation showed better agreement with natural vegetation maps when trait variability was included in JSBACH (Verheijen et al., 2013).

The second approach is to implement trait variability based on trade-offs between traits and evolutionary rules to determine the survival of the fittest trait combinations for a set of environmental conditions (Kleidon and Mooney, 2000; Langan et al., 2017; Scheiter et al., 2013). Scheiter et al. (2013) advocated the implementation of ideas derived from coexistence theory (Chesson, 2000) and community assembly theory (Webb et al., 2010) into process-based DGVMs. Information on trait trade-offs, including co-varying above- and below-ground traits (Freschet et al., 2010; Sloan et al., 2013) and on trait impacts on carbon fluxes (Cornelissen et al., 2007; Freschet et al., 2012) are already available and can foster the development of DGVMs based on eco-evolutionary principles. This require a detailed quantitative understanding of different allometric relationships to predict differences in above- and below-ground biomass in different plant communities. A comprehensive understanding of how different trade-offs relate to different plant architectures (for example between single stem and multi-stemmed woody plants, lianas, bamboo) would provide additional insights to structural details of growth forms. Such a modeling approach would sidestep the inclusion of many additional PFTs into DGVMs because community assembly would select plant growth strategies that are appropriate for given environmental conditions.

The availability of functional and structural plant trait data from global trait database such as TRY (Kattge et al., 2011), GIVD (Dengler et al., 2011) and sDIV (Purschke et al., 2015), can facilitate the addition

of new vegetation types and the parameterization of their ecological functions. While such information is partially available, it has not yet been compiled in an eco-evolutionary-based optimality approach for South Asian ecosystem. Nonetheless, it seems feasible to incorporate variable-trait approaches to represent growth forms for the modeling of vegetation dynamics, and carbon and nutrient cycling. Improving our representation of land cover therefore improves our understanding of the Earth system.

10. Conclusions

South Asia is the most populated part of the world, which implies high pressure on vegetation and biodiversity. Climate change and present-day land use pose threat on the future of many South Asian ecosystems. Their future trajectories are highly uncertain and DGVMs can be used to explore these climate-vegetation interactions. DGVMs have become an indispensable tool to formulate strategies to mitigate global change impacts on ecosystems and they have a wide range of potential applications for understanding diversity, biosphere-atmosphere interactions under different future climate and management scenarios (for example, elevated atmospheric CO_2, fire or herbivory (Harris et al., 2016; Harrison and Prentice, 2003; Midgley and Bond, 2015)). Improving the representation of land cover, fire and other anthropogenic factors like ozone pollution in DGVMs therefore contributes to improve our understanding of the Earth system.

Heterogeneous environments and floral distributions necessitate special attention to account for the different vegetation types and growth forms such as shrubs, lianas and bamboos. All of these vegetation types and growth forms have different structure and ecosystem functions. Current PFT schemes in DGVMs should be expanded to incorporate different communities and the eco-physiological process governing competition for resources. Improving the current generation of DGVMs both globally and at regional scale needs the combined effort of physiologist, ecologists and modelers to develop an understanding of the process explaining observed vegetation patterns. Processes such as carbon allocation, phenology, competition and disturbance in DGVMs are, in our opinion, the great challenges for improving the models. We also suggest that the incorporation of whole–plant hydraulic strategies into the representation of tropical dry and wet deciduous trees in DGVMs would improve simulations of water and carbon fluxes. To test the potential for model improvement, modelers should seek to include the discussed growth forms within a broad variety of trait-based dynamic vegetation models. Furthermore, the DGVM community needs to continue to incorporate knowledge from experimental studies on the ecophysiological responses to environmental changes, eco-evolutionary principles of tropical ecosystems and observations from the functional structure of plants into the models. This would further require field and validation studies to advance our ecological understanding of specific growth forms.

In summary, we claim that seven major challenges need to be addressed for improved modeling of South Asia's biome diversity.

- Distinction between wet and dry forest types, both in deciduous and evergreen forests.
- Representation of vegetation types and growth forms native to South Asia such as bamboo, mangroves, shrubs, thickets and lianas using FT and PFT approaches.
- Representation of topography to account for spatial heterogeneity in vegetation types along the mountains of South Asia.
- Incorporation of anthropogenic disturbance.
- Collection of eco-physiological data for improved ecosystem understanding; aggregation into databases and development of advanced data-model fusion techniques.
- Generation of high resolution environmental data (climate and soil) for driving DGVMs.
- Integration of observed plant trait variability into DGVMs.

Making effective use of our knowledge on South Asian ecosystems to improve DGVMs should be of high priority for more reliable projections of the future of these diverse ecosystems.

Acknowledgments

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